

THE TAXONOMY OF *PINUS FLEXILIS* AND *P. STROBIFORMIS*¹

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James (1823), who participated in the expeditionary search of the Rocky Mountains in the company of Lieutenant S. H. Long, observed at least two undescribed Western species of pine that were new to science. One consequence of his exploration of the eastern slopes of Pike's Peak was his description of *Pinus flexilis* from living material alone. The ensuing nomenclatural disorder involving the *Pinus flexilis* complex has created an interesting, but confusing array of nomenclatural problems. Perhaps the primary cause for the dilemma is the resemblance of vegetative features and the growth habit of the "Flexiles" group of pines to others within the North American five-leaved *Strobus* subgenus. Under less than optimal conditions of growth and in their juvenile stages they appear very similar indeed.

In the present paper, we will attempt to present a historical and contemporary review of *P. flexilis* James and *P. strobiformis* Engelm., two North American members of the subsection *Strobi* (*sensu* Little & Critchfield 1969), as well as to designate the neotype of *P. flexilis*.

HISTORICAL

Pinus flexilis

Although James gave a description of *P. flexilis* in his field notes, no herbarium samples were collected nor did he present a Latin diagnosis with his published description of 1823. Engelmann (1863), however, did publish a Latin diagnosis of *P. flexilis* and also emended the morphological inconsistencies that appeared in James' description. Earlier familiarization with *P. aristata* Engelm. led Engelmann (Parry and Engelmann 1862) to judge that James had observed both *P. flexilis* and *P. aristata* either side by side or perhaps with branches intertwined, for

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the prominent, armed, cone umbos noted by James (1823) is indicative of P. aristata and not P. flexilis.

Fortunately, Engelmann's (1863) accurate analysis clarified some additional confusion generated by Nuttall (1853, III p.107) by his inaccurate text and dismaying illustration. Engelmann, however, did not comment on Nuttall's work nor did he discuss Hooker's (1838, II p.161) contribution of P. lambertina var. β . Hooker, which in turn was based upon Drummond's (1830) field notes of five-leaved pines he observed in Canada while portaging from the Red Deer River to the Columbia at "Height of Land." Drummond's notes describe a taxon that either could be P. flexilis or P. albicaulis Engelm., for the cones he observed were damaged beyond recognition rodents or birds. The geographic locale, orogeny and elevation, however, suggest the trees were P. albicaulis. Endlicher (1847, p.150), not withstanding some reservation about Hooker's interpretation, established P. lambertiana variety β ("brevifolia, foliis brevioribus, rigidioribus, Hook. l.c."), but Endlicher's new combination gained little acceptance.

Further nomenclatural confusion arose when Carriere (1855, pp.309-310) attributed authorship of both P. flexilis and P. strobiformis to Wislizenus. This error probably arose because Engelmann's 1848 article appeared as one of the contributions within a book identified with Wislizenus as author-editor.

Pinus strobiformis

During Dr. Wislizenus' travels from Chihuahua westward to the vicinity of Cosihuiriachi and the Porphyry Mountains, he discovered a large number of undescribed plants. On the highest peaks, at elevations of about 8,000 feet, Wislizenus observed large pines 100 to 130 feet tall which bore resemblance to both P. flexilis and P. strobus L. This unknown pine was later named by Engelmann as P. strobiformis (1848). This perfectly valid species name, however, was apparently abandoned by Engelmann since it is conspicuously absent from his later publications (1878, 1880, 1882). Shaw (1909, p.11) reasoned that Engelmann, after learning of Ehrenberg's earlier (1838) description of Pinus ayachuete Ehren., assumed that the P. strobiformis of Chihuahua was the same taxon as Ehrenberg's P. ayachuete of Omitlan, Guerro. Since Engelmann had no cones to compare, he probably thought his species was synonymous with Ehrenberg's. Parlatores (1968, pp.406-407) cites P. strobiformis (sic) as a synonym of P. ayachuete and lists further collection sites in the northern states of Mexico for this species.

After abandoning P. strobiformis as the epithet for the trees found in northern Mexico, Engelmann (1878), in describing specimens collected by Wheeler's Expedition in Arizona reduced various forms which displayed some of the characteristics he attributed to P. strobiformis to varieties of P. flexilis. These characteristics included serrulation of leaves, reduction in number or lack of stomatal rows on the dorsal leaf surface, elongation of the cones, and elongation and reflexion of cone scales.

His varieties, based on materials from Arizona were collected from orographic sites where environmental conditions permit phenotypic development leading to intermediate morphological characters between P. flexilis and P. strobiformis. The present authors have collected material from all the higher peaks in Arizona and have gathered specimens similar to those described by Engelmann (1878), but more important, have also observed altitudinal change from typical P. strobiformis to P. flexilis as elevation increases. At higher elevations there usually is a preponderance of P. flexilis-like individuals but occasionally with an admixture of P. strobiformis. In short, all of Engelmann's varieties can be found on either a single mountain or on any combination of peaks in southeastern Arizona. Similar variation patterns exist in New Mexico.

Engelmann, as a prelude to his "Revision of the genus Pinus" was experimenting with "varietal taxonomy" which he soon abandoned, but his 1978 paper proposed (sans-Latin) the following three varieties:

1. Pinus flexilis var. α serrulata Engelm. "Leaves slender, slightly and distantly serrulate, and as in the following varieties with few or scarcely any stomata on the back; cone of the ordinary form."

The voucher specimen (Rothrock 654) for the above description consists of foliage, twig and fruiting materials, all of which bear strong resemblances to the P. flexilis-like materials found at higher elevations in Arizona and New Mexico. Materials collected by the senior author at 9700 feet on the west side of Mr. Graham, Arizona are almost identical to Rothrock's 1874 collection from the same area but at 9600 feet.

2. Pinus flexilis var. β macrocarpa Engelm. "Leaves slender, entire; cones cylindric, 6-8 inches long $2\frac{1}{2}$ inches in diameter, the apophysis of the scales short, rounded."

This material collected by Ferdinand Bischoff of Wheeler's 1871 expedition to the San Francisco Mountains of Arizona consists of foliage, twigs, and cone scales. No intact cone exists at present. Similar specimens were observed and collected by the senior author (Andresen 2121) at 9,000 feet on the west side of Humphrey's Peak in the San Franciscos. The cone scales of var. β are intermediate between vars. α and γ and are also intermediate within the clinal array of the P. flexilis-strobiformis complex of Arizona and New Mexico.

3. Pinus flexilis var. γ reflexa Engelm. "leaves as in last β ; cones ovate-cylindrical, about four inches long; apophysis elongated, reflexed."

Voucher materials for the above consist of three related herbarium sheets. The first (MO 1635443) includes a typical P. strobiformis cone

but in an immature stage collected (collector unknown) on 13 August, 1874. Although only four inches long, the elongated ovuliferous scales are strongly reflexed. An old tag attached to the cone reads "P. ayacahuite" (the ayacahuite had been crossed out and was replaced by flexilis var. squarosa 654 8/13 1874). The second sheet is similar to the first sans cone but includes "654=1001". And the third sheet numbered as "1001" bears materials labeled as originating from the Sanoita Valley which passes to the southeast and south of the Santa Rita Mountains. We suggest that the first two sheets were collected in the Madera Canyon drainage on the northwest side of the Santa Ritas and the third sheet was gathered either on the southeastern side of the Santa Ritas or on the northwest side of the Patagonia Mountains, with the former choice as the most likely.

Engelmann (1878) remarked that the cone of the third sheet, 1001, resembled P. koraiensis Sieb. et Zucc., or a small example of P. ayacahuite. Interestingly, on sheet 1001, is the penciled remark in Engelmann-like script "P. ayacahuite var. borealis" which was not published.

For some obscure reason, Engelmann (1880) chose not to include any of his varieties of P. flexilis or P. strobiformis in his "Revision of the Genus Pinus". He did, however, include the very questionable P. bonaparteae Carriere within his section Strobi. Shortly afterward, though, he (Engelmann 1882) reduced P. reflexa Engelm. to an altitudinal variant of P. flexilis hence P. flexilis var. reflexa Engelm. Perhaps he observed additional specimens or notes about the flowering habit of his P. reflexa for he wrote "Pinus reflexa n. sp. (P. flexilis. Eng. in Rothrock's Rep. Bot. Exp. Wheeler) proves to be quite distinct from "flexilis" not only by the reflexed scales of the cone, but also and principally by the long peduncled cylindric female aments, erect in the first, recurved in the second year, which associate it with the true Strobi, while the large wingless seeds distinguish it from the other species of that section."

His line of reasoning is difficult to follow for in the true Strobi (sensu Eustrobi Engelm. 1880) he includes P. albiculis and P. pygmaea both of which bear sessile and upright cones with wingless seed as well as P. flexilis whose cones may be sessile or sub-sessile but are always pendant.

The nomenclature was accepted by Coulter and Rose (1886) with a confirmation of species separation based on leaf anatomy. After examining specimens collected by Pringle in 1887 in the same area where Wislizenus collected the specimen described by Engelmann as P. strobiformis, Sargent (1889) concluded that P. strobiformis was probably only a northern form of P. ayacahuite with short leaves and small cones. Three years later, Lemon (1892 p.4), through an interpretive error, credited P. ayacahuite var. strobiformis to Sargent. The assignment was created by a liberal interpretation of Sargent's (1889) opinion of P. reflexa Engelm. vis. "Mr. Pringle rediscovered two years ago Engelmann's Pinus strobiformis on the mountains of Chihuahua, in the very region where Wislizenus first found it, and his specimens who that Pinus reflexa cannot be separated from the Mexican tree which was known previously from a single cone only. It will be found perhaps that Pinus strobiformis is merely a northern

form with short leaves, and small cones, of the widely distributed Pinus ayacahuite [sic.] Erh. The two are certainly very closely related and are not readily separated." Shaw (1909) attempted to correct the error by placing P. ayacahuite var. strobiformis Lemmon in synonymy with P. flexilis var. reflexa Engelm. In the interim, Sargent (1897 pp.33-34) recognized Pinus strobiformis Engelm. as a valid taxon, thus altering his 1889 opinion that P. strobiformis was only a form of P. ayacahuite.

Sudworth (1897 pp. 14-16) concurred with Sargent and placed P. flexilis var. reflexa Engelm., P. reflexa Engelm., and P. ayacahuite var. strobiformis Lemmon in synonymy with P. strobiformis Engelm. In addition, Sudworth listed P. flexilis var. α serrulata Engelm. as synonymous with P. flexilis and unfortunately presented Pinus flexilis var. magalocarpa Sudworth as a nomenclatural alternative to P. flexilis var. β macrocarpa Engelm. The following year, however, Sudworth (1898 p.14) ignored his P. flexilis var. magalocarpa and calling it by its common name reduced it to synonymy under P. flexilis. Apparently he also believed that P. ayacahuite was synonymous with P. strobiformis Engelm., for he indicated the range of the latter is southwestern United States, Mexico, and Guatamela.

By 1907, Voss decided P. ayacahuite var. reflexa Voss would be preferable to P. reflexa Engelm. Voss (1907) also subordinated P. strobiformis Engelm. to P. ayacahuite Ehrenb.

Shaw (1909) synthesized the existing literature and judged that P. strobiformis Engelm. was synonymous with the northern element of P. ayacahuite, and hence the name P. ayacahuite var. brachyptera Shaw. In his revision, P. flexilis and its var. reflexa were retained as valid taxa, with P. ayacahuite var. strobiformis Lemmon and P. strobiformis sensu Sudworth relegated to synonymy. Shaw evidently perceived that the P. strobiformis of Engelmann, Sudworth, and Sargent were not the same taxon. Later, Shaw (1914) modified his verdict and considered P. strobiformis Engelm. as synonymous with P. ayacahuite, and all other types previously mentioned as being only forms of P. flexilis. Only P. reflexa Engelm. and P. strobiformis Sargent are mentioned in his synonymy of P. flexilis.

Astutely, Sudworth (1917 pp. 12-13) suggested that P. strobiformis Engelm. bore chronological priority and submitted that this be the valid binomial. Although his logic was sound, few authors followed Sudworth's recommendation for the multitude of tree books and journal articles between 1917 and 1955 refer to this plant as either P. reflexa or P. flexilis. For example, Standley (1920 pp. 54-55) recognized P. flexilis and P. reflexa, but placed P. strobiformis in synonymy with P. ayacahuite.

In his second edition of the "Manual of the Trees of North America", Sargent (1922) omitted P. strobiformis Engelm., though he had included it earlier (Sargent 1905). Thus Sargent again reversed his thoughts -

and entered P. strobiformis Sarg. (non Engelm.) as a synonym for P. flexilis. The authoring of P. strobiformis by Sargent is difficult to comprehend.

CONTEMPORARY

Pinus flexilis and Pinus strobiformis

Martinez (1948 pp. 104-105) accepted Shaw's 1909 treatment of P. ayacahuite and recognized P. reflexa and P. flexilis as valid species. P. strobiformis Sudworth (non Engelm.) and P. ayacahuite var. strobiformis Lemmon (non Sargent) were placed in synonymy under P. reflexa. To round out his liberal interpretation of the white pines of Northern Mexico, Martinez, in an attempt to portray the relationships of the Eustrobi (sensu Shaw), also recognized numerous geographic locations for P. ayacahuite var. brachyptera. Martinez also proposed the hierarchical "Grupo Ayacahuite" with P. ayacahuite as the central element. Radiating from P. ayacahuite are P. lambertiana, P. strobis var. chiapenses (= P. chiapenses (Martinez) Andresen 1964), P. ayacahuite var. veitchii, and P. ayacahuite var. brachyptera. He also depicts the latter as an intermediate (inferior status) between P. ayacahuite and P. reflexa which in turn is linked to P. reflexa. Mirov (1953), using terpeno-chemical relationships as a criterion, believed that P. reflexa and P. ayacahuite are bridged by a series of intermediate forms (not yet chemically analyzed) and that there is a link with flexilis and monticola but only a remote connection with P. strobiformis and an undetermined link with P. lambertiana.

In an attempt to resurrect P. flexilis var. macrocarpa, Douglass (1958) decided that this variety was a morphological link between P. flexilis var. flexilis and P. flexilis var. reflexa and that the three were closely related. She also suggested a "very slight" difference between the vars. of P. ayacahuite and P. flexilis, but her conclusions are unsupported by genetical evidence or any other types of biological data.

Recently, Gaussen (1960 pp. 202-205) recognized as discrete species P. flexilis, P. reflexa and P. strobiformis, with the latter as equivalent to P. ayacahuite var. brachyptera. Little (In Soto, Barrett and Little 1962 p. 88), writing on the classification of P. flexilis and P. strobiformis, indicated that these are the "correct" combinations and that earlier opinions (Little 1950 pp. 13-14; 1953 pp. 265-266) recognizing P. flexilis var. reflexa were now altered. And finally, Critchfield and Little (1966 pp. 6, 7) reiterated Little's 1962 opinion.

TAXONOMY

Pinus flexilis James

Pinus flexilis James, Account of an expedition from Pittsburg to the Rocky Mountains. Vol. 2 pp. 34-35 (1823); Sargent (1897).

Pinus lambertiana var. β Hooker, Flora Boreali-Americana. Vol. 2 p. 161 (1890).

Pinus lambertiana var. β brevifolia Endl., Synopsis coniferarum. p. 150 (1847).

Apinus flexilis (James) Rydb., Torrey Bot. Club. Bul. Vol. 32 p. 598 (1905).

Morphologic description is essentially correct in Sargent (1897).

Distribution: Rocky Mountains south from head waters of Saskatchewan River through Idaho, Montana, Wyoming, Colorado. Mountain ranges of Nevada, Sierra Nevada, and Peaks of southwestern California. Rare and local in Wallawa Mountains, Oregon, southwestern Nebraska, western South Dakota, and southwestern North Dakota. On high peaks of Arizona and New Mexico to the Guadalupe of Texas. Not in Mexico!! (See range map in Critchfield and Little 1966).

Specimens examined:

CANADA: ALBERTA: 50° 23' N. Lat.; 114° 40' W. Long., 1550 m alt., 30 July 1961, Andresen, Andresen and March A1174 (MSC)

UNITED STATES: ARIZONA: Navajo Mountains, 10,500 ft. alt., July 1933, Darsie s.n. (MO); CALIFORNIA: White Mountain Ranger Dist., Inyo Nat. For., 37° 23' N. Lat., 118° 11' Long., 2980 m alt., 31 July 1962, Andresen A1702 (MSC); San Geronio Ranger Dist., San Bernardino Nat. For., 34° 07' N. Lat., 116° 51' W. Long., 3070 m alt. 4 Aug. 1962, Andresen and Lord A1721 (MSC); COLORADO: Pike's Peak, (probably early October) 1862, Parry s.n. (MO); Summit, Deer Mountain, Larimer Co., 13 Aug. 1927 Woodson Jr. 1882 (MO) Teller County, western flank of Pike's Peak, on Fourmile Creek just north of junction with Oil Creek, Lat. 38° 51' N. Long. 105° 10' W. 8800 Ft. alt. 19 October 1965, Hawksworth and Stewart 831 (SIU); IDAHO: Pine Spring Pahsimers River Valley, Custer Co., 2 Aug. 1917, Eggleston 14002 (MO); MONTANA: Gros Bentes Fork, 12 June 1860, Hayden s.n. (MO) Old Marias Pass, 6000 ft. alt., Aug. 1883, Sargent s.n. (MO); NEBRASKA: Bad Lands, Sept. 1955, Hayden s.n. (MO); Polecreek of the Platte River, July 1856, Engelmann s.n. (MO); NEVADA: Austin Ranger District, Toiyabe Nat. For., 39° 23' N. Lat., 117° 04' W. Long., 2540 m alt., 20 July 1962, Andresen and Andresen Jr. A1659 (MSC); NORTH DAKOTA: north of Marmarth, Slope Co., 46° 28' N. Lat., 103° 55' W. Long., 763 m alt., 21 July 1961. Andresen, Andresen, Andresen Jr. A1049 (MSC); OREGON: Joseph Ranger District, Wallawa-Whitman Nat. For., 45° 17' N. Lat., 117° 19' W. Long., 1800 m alt., 3 Aug. 1961, Andresen and Miller A1196 (MSC); SOUTH DAKOTA: "Needles", Custer State Park, Pennington Co., 20 June 1929, Palmer 37408 (MO); UTAH: Salina Ranger District, Fish Lake Nat. For., 38° 57' N. Lat., 111° 39' W. Long.,

2560 m alt., 14 July 1962, Andresen, Andresen Jr., and Hill Al616 (MSC); WYOMING: Loomis Creek, Natrona Co., 3 July 1901, Goodding 185 (MO).

As indicated earlier, James did not prepare any plant specimens of P. flexilis when he observed his new pine on 14 July 1820. In his description, James (1823) probably referred to immature but nearly full sized cones whose ovules were fertilized in the spring of 1820. His notation of "the stobiles erect, composed of large unarmed scales, being somewhat smaller than those of P. rigida, but similar in shape and exuding a great quantity of resin." is an accurate description of sessile, "green" cones (at times aborted or distorted by insect attack) that the senior author has also observed about mid-July. In spite of Engelmann's (1863) opinion that James confounded P. aristata and P. flexilis in his description, we contend that James observed and described P. flexilis by itself without confusion with P. aristata.

Since no type specimens were collected we hereby propose a neotype (Lanjouw et. al., 1961: Art. 7) based on the following material: COLORADO: El Paso County, eastern flank of Pike's Peak, $\frac{1}{4}$ mile north of Ruxton Park Lat. $38^{\circ} 51' N$. Long. $104^{\circ} 58' W$. 9676 ft. alt. 14 July 1966, Andresen, Andresen, Barger A2125.

The neotype and mature cone which includes a conelet is housed at Southern Illinois University. Other specimens with foliage sprays and mature cones are on file at A, MO, MSC, and NA.

The neotype material is probably from the same locality or station visited by James (1823). From his description and map it seems that he and his party were in the Pike's Peak area from 11 through 15 July 1820 primarily to determine the elevation of Pike's Peak. The ascent of Pike's Peak and the resultant discovery of P. flexilis were ancillary to the triangulation exercise.

The following summary of James' trip is provided to help establish the route of James' ascent and possible points of observation of P. flexilis: After leaving the base camp near the confluence of Cheyenne and Fountain Creeks, James, his party of four men and Lt. Swift with his guide rode until 11 a.m. on the 13th. Lt. Swift set up his triangulation station, the horses were tethered and James, the guide and four men walked until noon when they encountered Manitou Springs. After lunch they ascended the Ruxton Creek drainage and probably camped near the present Ruxton Park. The next morning James described the view of the peak at a spot (possible the present hamlet of Mountain View) east southeast of the peak. By noon of the 14th they had reached and passed timber line and at 4 p.m. had attained the summit. After half an hour at the summit the party descended and camped at timber line. By noon of the 15th they were again at Manitou Springs without most of their baggage which had burned when a wild fire spread from their unattended campfire. No plant collections were made (primarily because of time shortage) but numerous new species were described and many left undescribed because of a shortage of time. The major point, however, is

that the ascent was up the eastern flank and slope of Pike's Peak; no collections or observations other than physiognomic or geologic were made of the other three slopes.

Pinus strobiformis Engelm.

Pinus strobiformis Engelm., Sketch of the botany of Dr. A. Wislizenus's expedition. Sen. Misc. Doc. No. 26 (1848).

Pinus flexilis var. α serrulata Engelm. Coniferae of Wheeler's expedition. In Report upon U.S. geographical surveys west of the one hundredth meridian. Vol. VI p.258 (1878).

Pinus flexilis var. β macrocarpa Engelm. Coniferae of Wheeler's expedition in Report upon U.S. geographical surveys west of the one hundredth meridian. Vol. VI p. 258 (1878).

Pinus flexilis var. γ reflexa Engelm. Coniferae of Wheeler's expedition in Report upon U.S. geographical surveys west of the one hundredth meridian. Vol. VI p. 258 (1878).

Pinus flexilis var. magalocarpa Sudworth. Nomenclature of the arborescent flora of the United States, USDA, Division of For. Bull. No. 14:17 (1897).

Pinus reflexa Engelm. Bot. Gaz. 7: 4 (1882)

Pinus ayacahuite Ehrenb. Linnaea. 12:492 (1838)

Pinus ayacahuite var. strobiformis Sargent ex Lemmon. Handbook of west-American cone-bearers. 4 (1892).

Pinus ayacahuite var. reflexa Voss. Deut. Dendrol. Gessell. Mitt. Vol. 16 p. 92 1907).

Pinus ayacahuite var. brachyptera Shaw. Pines of Mexico Pub. Arnold Arb. No. 1:11 1909.

Morphologic description of Sargent (1897) essentially correct but from our field observations it should be noted that second-year immature cone may be green or purple to lavender in color.

Distribution: Southern Colorado, Arizona, New Mexico, western Texas, the Sierra Madre Occidental of Chihuahua, Durango, Nayarit, Sinola, and Sonora; and the Sierra Madre Oriental of Coahuila, Nuevo Leon, San Luis Potosi, and Tamaulipa.

Specimens examined:

MEXICO: CHIHUAHUA: "Cosiquinachi" 17 September, 1846, Wislizenus 155 (MO) (Holotype); San Pedro Springs, Dec. 1906, Goodding 2114 (MO); DURANGO: Mesa de Sandia, "1903-07" Shaw "Set 8" (MO) (as P. ayacahuite

var. brachyptera); Cerro de Viejo, 15 mi. W. Dulces Nombres, Zaragoza, 2800 m. alt., 18 Aug., 1948, Meyer and Rogers 3002 (MO) (as P. ayacahuite var. brachyptera [brachyptera] UNITED STATES: ARIZONA: Chiricahua Mts., Barfoot Park, 8200 ft. alt., 20 Oct., 1906, Blumer 1311 (MO); Santa Catalina Mts., 7000 ft. alt., 3 Oct., 1937, Darrow s.n. (MO); Santa Rita Mts., 13 Aug., 1871, Rothrock 654 (MO) (Holotype); Santa Rita Mts. 6500-7500 ft. alt., 27 September, 1880, Sargent s.n. (MO); Santa Rita Mts., 6000-8000 ft. alt., 28 May, 1881, Pringle s.n., (MO) (as P. reflexa Engelm.); Indefinite, 13 Aug., 1874, collector unknown, 1635443 (MO); Indefinite 13 Aug. 1874, collector unknown, 654 (MO); Sanoita Valley, 13 Aug. 1874, collector unknown 1001 (MO). COLORADO: La Plata River 1 to 4 mi. N. of May Day 37° 22' N. Lat. 108° 04' W. Long 9000 ft. alt., 12 Sept. 1964, Critchfield and Steinhoff 22 t 24 (CU); S. Fork of Rio Grande River, 215 mi S.W. of Baxterville, 37° 39' N. Lat. 106° 39.7' W. Long. 8300 ft. alt. 15 Sept. 1964 Critchfield and Steinhoff 2021 (CU). NEW MEXICO: Cloudcroft, 6000 ft. alt., 9 July 1909, von Schrenk s.n. (MO) (as P. flexilis); Mogollon Mts., Catron Co., 7000 ft. alt., 26 June 1947, Meyer and Meyer 2212 (MO); TEXAS: Davis Mts., Jeff Davis Co., 2300 m alt., 1 June, 1928, Palmer 34281 (MBG) (as P. flexilis var. reflexa Engelm.); McKittrick Canyon, Guadalupe Mts., Culberson Co., 2400 m alt., 17 July 1931; Moore and Steyermark 3469 (MO) (as P. flexilis).

DISCUSSION

Pinus strobiformis Engelm. as considered here, is a distinct mountain inhabitant of the northern states of Mexico, western Texas, and southern Arizona and New Mexico, but as it is found farther north the higher elevational forms assume the morphology of P. flexilis. Hybrid swarms of P. flexilis and P. strobiformis are also found at higher elevations and with some representatives at 8000 ft., in southern Colorado. Although progeny tests (Steinhoff 1964; Steinhoff and Andresen 1971) revealed apomictic taxa, further investigations of putative hybrids and introgressed populations are called for. Successful artificial hybrids of P. flexilis and P. strobiformis have been produced, but their development under various environmental conditions has not yet been attempted. Also, the manner in which natural selection acts upon segregating hybrid progeny is not well understood.

Recently, an excellent series of maps (Critchfield and Little, 1966) has been released which depicts the geographic distribution of P. flexilis, P. strobiformis, and P. ayacahuite. In addition, their revision (Little and Critchfield 1969) of the genus Pinus assembles within subsection Strobi Loud. the above three taxa, and by including P. armandii Franch. with Strobi, effectively disposed of group Flexiles Shaw. More important, however, are the opinions of Critchfield and Little that P. strobiformis and P. ayacahuite are closely allied, which ties the three taxa into a taxonomic complex worthy of more intensive study.

Earlier chemotaxonomic work by Mirov (1953) linked P. strobiformis [P. reflexa] to P. ayacahuite through a series of intermediate forms whose biochemistry awaits expanded investigation. He placed P. flexilis in a separate chemical group, but suggested that P. parviflora Sieb. and

Zucc. formed a link between the former and P. strobiformis.

Considering recent advances in biochemical and numerical systematics, it is now appropriate to determine the taximetric and genetic affinities of the north to south complex of P. flexilis, P. strobiformis, and P. ayacahuite.

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